TMESIPTERIS IN THE SOLOMON ISLANDS

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ABSTRACT

Studies of recently collected material of *Tmesipteris* have revealed a wider range of morphological, anatomical and ecological variation than hitherto known in the genus from the Solomon Islands. Three species, *T. oblanceolata* Copel., *T. tannensis* (Spreng.) Bernh. and a new species, **T. solomonensis** A.F. Braithw., are described. The most interesting is *T. oblanceolata* Copel., an erect partially terrestrial species which closely resembles in many respects the New Caledonian endemic species *T. vieillardii* Dang.

INTRODUCTION

Tmesipteris was first collected in the Solomon Islands by Kajewski in the early nineteen thirties from Tatuve Mountain, Guadalcanal, and subsequently described by Copeland (1936) as *Tmesipteris oblanceolata*. Since Kajewski's original collection no further specimens have been recorded or collected for over thirty years so that our knowledge of this small genus in the Solomon's group of islands has remained incomplete. During the 1965 Royal Society Expedition to the Solomon Islands the genus was rediscovered and several new gatherings were made from Mt Popomanaseu, Guadalcanal, and Kolambangara in the New Georgia Group, where it was found not infrequently in the mossy forest at higher altitudes. Studies of this new material have revealed a wider range of morphological and ecological variation of the genus in the Solomon Islands than hitherto known. Three different forms can be recognised and the ecology, morphology and anatomy of each of these forms will be described in the present paper.

It is well known and accepted that *Tmesipteris* is found in several different forms but there is lack of agreement amongst taxonomists concerning the status of these variants. Some authors have preferred to place them all under one species, *T. tannensis* (Spreng.) Bernh., while others, notably Endlicher (1833, 1839), Dangeard (1891), Sahni (1925), Wakefield (1943) and Barber (1954) have described various forms as different species based mainly on morphological characters combined in some instances (Dangeard, l.c.; Sahni, l.c.) with anatomical characters. Barber (1957) presented cytological and other evidence to support the recognition of six morphologically distinguishable populations from Australia, Tasmania and New Zealand as good reproductively isolated species. Although no direct cytological or genetical evidence is available for the three forms from the Solomon Islands each of them is considered to be distinct enough in its ecology, morphology and anatomy to merit its recognition as a species. A brief summary of the principal characteristics of each species is given in Table 1.

The most interesting is *T. oblanceolata* Copel., an erect partially terrestrial species, which in its external morphology and anatomy closely resembles the New Caledonian endemic species, *T. vieillardii* Dang. The two remaining forms are both epiphytic on tree ferns, one being placed under *T. tannensis*, while the other is described as a new species, *T. solomonensis*, which resembles in some respects *T. lanceolata* Dang. from New Caledonia.

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TABLE 1

Summary of principal characteristics of T. oblanceolata

Species	Coll. No.	Habitat	Length of plant (cm)	Transition region (cm)
T. oblanceolata	RSS4782	terrestrial	20 – 35	8 – 13
	RSS4827	epiphyte on *Dicksonia sciurus*	19 – 21	7 – 9
T. tannensis	RSS4420	epiphyte on *Dicksonia sciurus*	7 – 16	1.5 – 3
	RSS4779	epiphyte on *Dicksonia sciurus*	6 – 14	1 – 3
	RSS4783	epiphyte on *Dicksonia sciurus*	8 – 16	1.5 – 3.5
T. solomonensis	RSS4824	epiphyte on *Cyathea solomonensis*	5 – 10	0.75 – 1.5

* Each entry represents the mean of 100 measurements from different plants.

T. tannensis and T. solomonensis

Anatomy of transition region	Leaves	Mean length of stomata (μm)*	Sporophylls	Mean spore size (μm)*
collenchymatous pith with medullary xylem	radially arranged; 10-15x3-4.5mm; oblanceolate	122 124 126 128	In distal half of leafy shoot only; approx. same length as sterile leaves	80 X 32 83 X 35
collenchymatous pith with medullary xylem	radially arranged; 8-12x2.5-3mm; oblanceolate	119 124 125	In distal half of leafy shoot only; approx. same length as sterile leaves	86 X 36
sclerenchymatous pith without medullary xylem	radially arranged; 9-16x3.5-5.5mm; oblong-elliptic	107 109 110 116	In middle or throughout leafy shoot; same length as sterile leaves	74 X 29 75 X 30
sclerenchymatous pith without medullary xylem	radially arranged; 8-14x3.5-4.5mm; oblong-elliptic	107 111 112 113	Throughout leafy shoot; same length as sterile leaves	–
sclerenchymatous pith without medullary xylem	radially arranged; 10-15x3-5mm; oblong-elliptic	102 108 116 117	Throughout leafy shoot; same length as sterile leaves	–
very small sclerenchymatous pith without medullary xylem	arranged in two lateral rows; 10-16x3-4mm; ovate-lanceolate	90 96 98 99	In proximal half of leafy shoot often only at the base; shorter than sterile leaves	63 X 23 64 X 23

T. OBLANCEOLATA COPEL.

Copeland (1936) distinguished this species by its oblanceolate leaves which are broadest in the distal half with broadly rounded apices and approximately symmetrical in the proximal half. I follow Copeland in recognising this species but the new material at my disposal has made it possible to amplify considerably its distinctive features. In addition to the leaf characters, other features which distinguish this species from the remaining forms of *Tmesipteris* in the Solomon Islands include its partially terrestrial habitat, long transition region and a large collenchymatous pith with medullary xylem in the transition region. The account which follows is based on two gatherings (RSS4782 and RSS4827) from Mt Popomanaseu, Guadalcanal.

Ecology: The few ecological observations available suggest this species is somewhat variable in its habitat. Of the two recent collections, one was terrestrial growing erect out of the moss around the base of a large tree trunk in mossy forest at 1520 metres (Plate XXIX C), while the other was epiphytic and semi-erect on the trunk of the tree fern, *Dicksonia sciurus* C. Chr., at 1155 metres. The type material and only other collection was found by Kajewski growing out of the moss covering stunted trees at an altitude of 1700 metres. It is clear from these records that this species is less closely associated with tree ferns than the other two species in the Solomon Islands, and that it appears to favour a mossy substrate on top of wood or soil.

Habit: The erect terrestrial plants possess long radially symmetrical shoots up to 32 cm high while the epiphytic plants are much shorter reaching only 21 cms. In both cases the basal transition region is much longer than in *T. tannensis* and *T. solomonensis*, representing more than a third of the total length of the shoot, and bears a larger number of small scale-like leaves. The leafy part of the shoot is made up of numerous closely packed sterile leaves and sporophylls (Plate XXIX D). In the living condition the plants are rather dark almost blue-green, particularly the terrestrial material.

Anatomy of the transition region: The most notable feature of the anatomy of *T. oblanceolata* is the presence of a large collenchymatous pith sometimes with medullary xylem in the lower parts of the aerial shoot. Medullary xylem has previously been reported in both the transition region and leafy shoot of *T. vieillardii* from New Caledonia (Sahni 1925), but in the present material it is found only near the base of the transition region. Apart from this difference, the general features of the anatomy of *T. oblanceolata* which are described below are virtually indistinguishable from those described and illustrated by Sahni (1925) for *T. vieillardii*.

In *T. oblanceolata* the solid core of tracheids of the rhizome becomes medullated at the base of the transition region, enlarges and splits into a variable number of groups of tracheids. As the stele expands the groups of tracheids form a ring of mesarch bundles surrounding a clearly defined pith which is made up of thickened slightly collenchymatous cells. Near the base of the transition region the xylem strands sometimes cut off groups of tracheids towards the centre of the shoot axis which then pass through the pith longitudinally for a short distance. One of these medullary strands can be clearly seen in the transverse section in Plate XXX C, cut at *c.* 1cm from the base of the transition region of the terrestrial material. The medullary strands are without protoxylem and apparently end blindly in the pith.

In both the terrestrial and epiphytic material the medullary xylem is small in amount and has so far only been found in the basal 1—2cm of the transition region. Among the terrestrial plants it was found in three of the four specimens which were

PLATE XXIX. *Tmesipteris* in the Solomon Islands. **A**: *T. solomonensis,* Guadalcanal, RSS4824, epiphytic on the trunk of Cyathea solomonensis; **B**: *T. tannensis,* Mt Popomanaseu, Guadalcanal, RSS4779, epiphytic on the trunk of Dicksonia sciurus; **C & D**: *T. oblanceolata,* Mt Popomanaseu, RSS4782, growing out of moss carpeting the base of a large tree trunk; **E**: *T. tannensis,* Kolambangara, New Georgia Group, RSS4420.

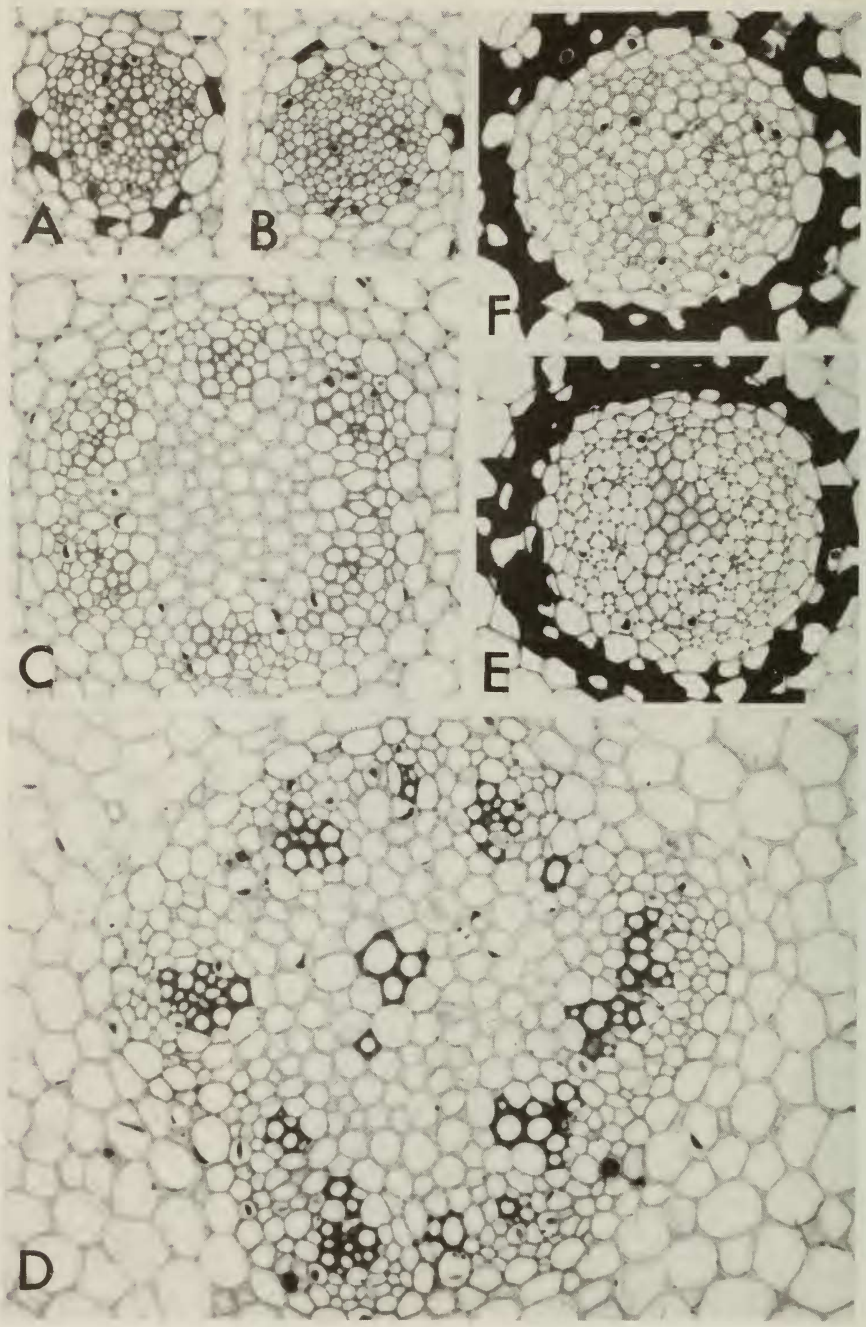


PLATE XXX. Transverse sections of the transition region of *Tmesipteris* from the Solomon Islands. All sections x100. **A** & **B**: *T. solomonensis,* RSS4824, A from the base and B from the top of the transition region; **C** & **D**: *T. oblanceolata,* RSS4782, C is from the base and D from the top of the transition region; **E** & **F**: *T. tannensis,* RSS4420, E is from the base and F from the top of the transition region.

sectioned and among the epiphytic material it was present in the single specimen which was available for sectioning. It has not been found in any material of *T. tannensis* or *T. solomonensis* which has been examined. It is, therefore, concluded that medullary xylem is a reasonably characteristic feature of the basal part of the transition region of *T. oblanceolata*.

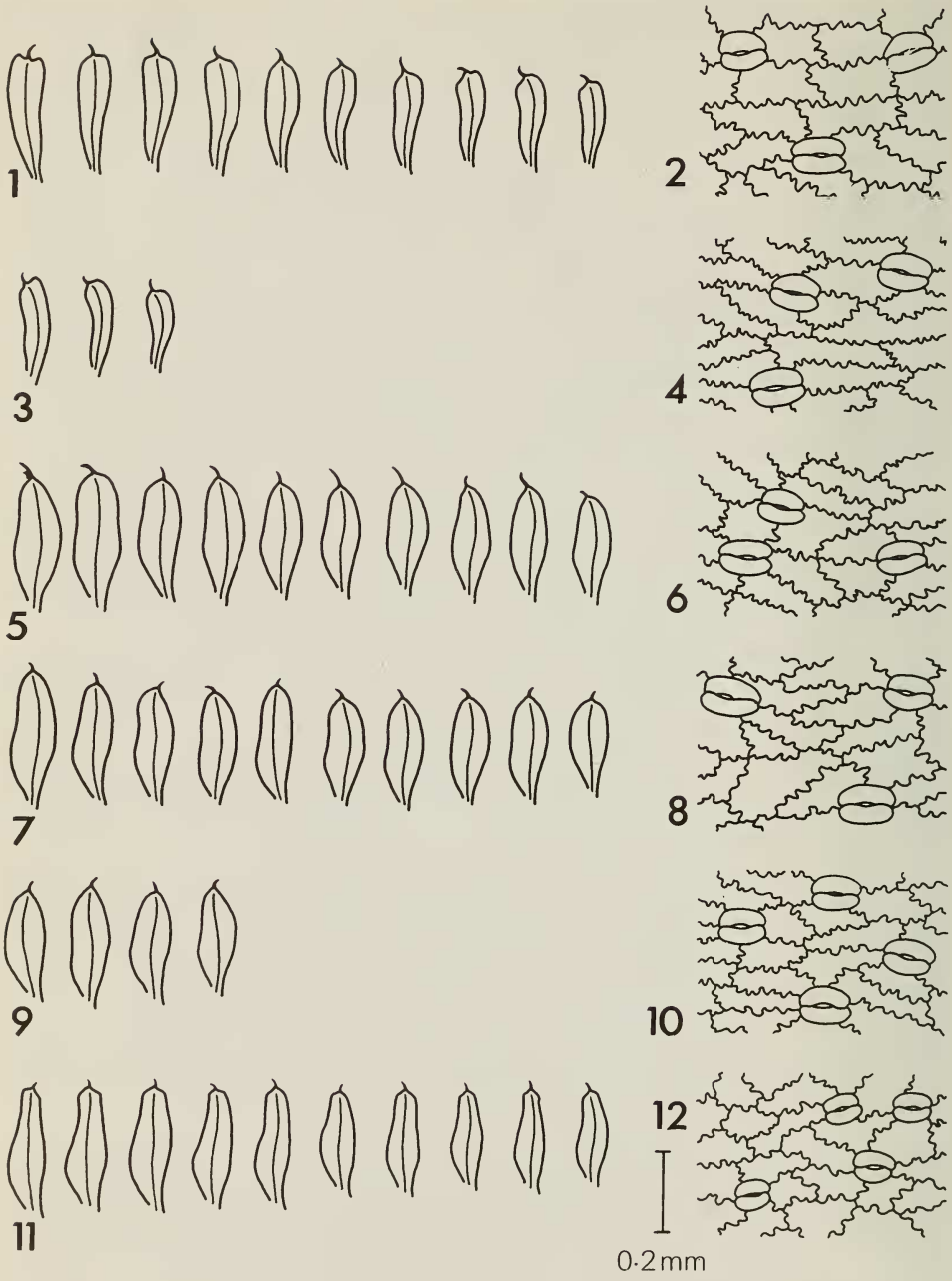
In the upper part of the transition region and the lower part of the leafy shoot the stele is made up of a ring of mesarch bundles, each with internal and external phloem surrounding a relatively large pith which is devoid of medullary xylem. A typical section from the top of the transition region (Plate XXX D) shows a pith, up to 10 cells across, made up of thick-walled collenchymatous cells surrounded by six strands of tracheids. The pith cells are more uniformly thickened and with much thicker cell walls than those near the base of the transition region. (Compare Plate XXX C & D). In longitudinal sections they are long and rather narrow with straight or oblique end walls and with numerous small, round, oval or slit-like pits in the side walls. They are quite different in appearance even in transverse sections from the fibre-like pith cells found in *T. tannensis* and *T. solomonensis*.

It is interesting to note that the dark material, usually referred to as phlobaphene or tannin anhydrides, which is commonly deposited in the cortical cells surrounding the stele in the rhizome and aerial shoots of *T. tannensis* and *T. solomonensis* is absent from the present material, except in the rhizome and immediately adjoining portion of the transition region.

Leaves and Sporophylls: The oblanceolate leaves are broadest in the distal half with broadly rounded mucronate apices and taper gradually towards the base (Figs 1 and 3). They are easily distinguished from the leaves of *T. tannensis* and *T. solomonensis* which, in contrast, are broadest about the middle and proximal halves of the leaves respectively. The epidermal cells and stomata (Figs 2 and 4) show no useful distinguishing features although the guard cells of the stomata tend to be longer than in either of the two other Solomons taxa (see Table 1).

The sporophylls tend to be confined to the upper part of the leafy shoot and are approximately the same length as the sterile leaves. The spores are the largest found amongst the material from the Solomon Islands (see Table 1). In the two spore samples available from the terrestrial material there is a small proportion of mis-shapen and apparently abortive spores. Abnormal spores have previously been reported by Sahni (1925) in spore samples from *T. vieillardii*. The significance of these observations is not at present clear but they perhaps indicate some cytological irregularity at meiosis in these plants. Unfortunately no cytological observations are available for the material.

Discussion: The material treated here as *T. oblanceolata* resembles closely the endemic terrestrial species, *T. vieillardii*, from New Caledonia. Both species share an erect terrestrial habit, a long transition region with numerous small scale leaves and a leafy shoot (dark green in colour) with many closely set leaves and sporophylls confined to the distal half. In addition the two species are anatomically virtually indistinguishable, both possessing a relatively large collenchymatous pith with medullary xylem in the transition region. The leaves of *T. vieillardii* are, however, narrow and strap-shaped with parallel sides and are always strongly falcate and recurved.



FIGURES 1—12. Leaves and epidermis of *Tmesipteris* from the Solomon Islands. Each leaf represents a different plant. 1—4: *T. oblanceolata,* 1 & 2 = RSS4782, 3 & 4 = RSS4827; 5—10: *T. tannensis,* 5 & 6 = RSS4420, 7 & 8 = RSS4779, 9 & 10 = RSS4783; 11 & 12: *T. solomonensis,* RSS4824. Leaves natural size.

T. TANNENSIS (SPR.) BERNH.

Tmesipteris tannensis is based on *Lycopodium tannense* Sprengel (1800, page 267) and it is doubtful whether any type specimen exists. It is therefore not certain that the Solomon Islands material to be described here is the same species. No Forster specimen from Tanna has been seen and the plant illustrated by Bernhardi (1801) possesses pointed synangia, a feature not present in the Solomons material. Despite this difference it is considered preferable to place this material here until the precise nature of the type material has been clarified in order to avoid describing a new species which in the final analysis may prove unnecessary.

T. tannensis is distinguished from *T. oblanceolata* by being always epiphytic on tree ferns and by its aerial shoots with a shorter transition region, less densely arranged oblong-elliptic leaves and smaller spores as well as by a number of anatomical features. The following observations are based on two gatherings from Mt Popomanaseu Guadalcanal (RSS4779, RSS4783) and one from Kolambangara, New Georgia Group (RSS4420, Plate XXIX E).

Ecology: T. tannensis is the commonest form of *Tmesipteris* in the Solomon Islands. It was found quite frequently on the trunks of *Dicksonia sciurus*, which is a common tree fern in the higher altitudes of the montane forest from 1200–2286 metres (Plate XXIX B). It is apparently confined to this species of tree fern in the Solomon Islands since extensive searching did not yield any specimens from *Cyathea* species even though these were often present in the same locality.

The specificity of any particular form of *Tmesipteris* for a tree fern species or group of species has never been recorded but it is noteworthy that a collection of almost identical material from Goodenough Island, New Guinea (Brass 24749,K) bears a collector's note indicating that it was only found on *Dicksonia* (species not specified) and never on *Cyathea* species which were present in the same locality.

Habit : The pendulous aerial shoots are shorter than those of *T. oblanceolata* with a short transition region representing only a fifth or sixth of the total length of the shoot. The leaves and sporophylls are radially arranged, as in *T. oblanceolata*, although there are sometimes a few sterile leaves at the apex of the shoot arranged in two rows. They are, however, much less densely arranged and consequently fewer in number than in the previous species.

Anatomy of the transition region: So far as the anatomy of the aerial shoot is concerned the main differences from *T. oblanceolata* lie in the sclerenchymatous nature and pitting of the pith cells and in the absence of medullary xylem from the pith in the transition region. Some of the principal features of the anatomy are illustrated in Plate XXX E & F, which show transverse sections from the lower and upper parts of the transition region respectively.

At the base of the transition region the solid core of tracheids of the rhizome expands and divides to form two or three mesarch bundles. Meanwhile groups of thickened, lignified fibre-like cells appear at the periphery of the stele (Plate XXX E). Moving upwards through the transition region the groups of tracheids gradually increase in size and divide further to form a ring of bundles and sclerenchymatous cells appear in the centre forming a pith. These pith cells are at first joined laterally to the fibre-like cells at the periphery of the stele but towards the top of the transition region the peripheral fibre-like cells disappear altogether so that a typical section from the top of the transition region shows a ring of five to seven mesarch bundles

surrounding a well defined pith made up of 15—20 sclerenchymatous cells (Plate XXX F). Each bundle is made up of a group of thin walled tracheids with lignified phloem cells on either side. The pith cells are narrow and fibre-like with numerous slit-like pits in the side walls and even in transverse sections are quite different in appearance from the collenchymatous pith cells of *T. oblanceolata.* No medullary xylem has been observed in the pith of the transition region. Phlobaphene is present in the inner cortical cells throughout the transition region and lower part of the leafy shoot.

Leaves and Sporophylls: The sterile leaves are somewhat unequal-sided at the base, oblong-elliptic, with a mucronate apex (Figs 5, 7, and 9). They are broadest in the middle of the leaf and are quite different in shape from those of *T. oblanceolata*, which are broadest towards the apex. The epidermal cells and stomata are shown in Figs 6, 8 and 10 and size of the guard cells of the stomata in Table 1. The guard cells are smaller than those of *T. oblanceolata* but otherwise the epidermal characters do not show any major distinguishing features.

The sporophylls are found in the middle or throughout the length of the aerial shoot and, as in *T. oblanceolata*, are approximately the same length as the sterile leaves. The synangia are rounded and the spores are smaller than those of *T. oblanceolata* (see Table 1).

Discussion: The morphology and anatomy of the Solomons plants matches very closely that of the material referred to *T. tannensis* var. *tannensis* by Sahni (1925) from New Caledonia. They are also virtually indistinguishable in their external morphology from a *Tmesipteris* collection seen from Goodenough Island, New Guinea, (Brass 24749, K).

A NEW SPECIES FROM GUADALCANAL

T. solomonensis A.F. Braithw. sp. nov. Planta epiphytica, 5—10 cm longa; pars transitionis 7.5—15 mm longis, 4—10 bracteis foliiformibus. Folia sterilia, bifaria praeter basem, herbacea 10—16 mm longa, 3—4 mm lata, ovato-lanceolata, apice truncato-mucronatis. Sporophyllae plerumque versum basem caulis foliosi, radialiter dispositae, foliis sterilibus breviores. Capsulae 2.5 x 1 mm, sphaericae; sporis 56 — 71 μm longis, 19 — 26 μm latis (ordo mediis 64 x 23 μm). (Plate XXIX A).

TYPE: Central Guadalcanal: Mt Popomanaseu, by path from Vunuvelakama to Tambulusu; epiphytic on *Cyathea solomonensis* Holttum in ridge-top forest; 1066m. Braithwaite RSS4824, 6 Nov. 1965. *Holotype, BM*; isotype K

Habit: The small pendulous plants possess light green rather delicate aerial shoots up to 10 cm long with a short transition region representing a sixth or seventh part of the whole shoot. In contrast to the two previous species almost all the sterile leaves are arranged in two lateral rows except for one or two near the base of the leafy part of the shoot which are often arranged radially. The radially arranged sporophylls occur between the base and middle of the leafy shoot.

Anatomy: The anatomy of the transition region of *T. solomonensis* is similar to that of *T. tannensis* and need not be described in detail here. Transverse sections from the lower and upper parts of the transition region are shown in Plate XXX A & B for comparison with the two previous species. It will be noted that the stele is very small and that the pith even at the top of the transition region is rather ill-defined and

consists of only a few sclerenchymatous cells. In longitudinal sections the pith cells are fibre-like with narrow slit-like pits. Surrounding the pith there are 3 or 4 mesarch bundles made up of thin walled tracheids with lignified phloem cells on either side. As in *T. tannensis* the cortical cells around the stele contain phlobaphene.

Leaves and Sporophylls: The sterile leaves are ovate-lanceolate with a mucronate somewhat truncate apex (Fig 11). They differ from the leaves of *T. oblanceolata* and *T. tannensis* by being broadest towards the base of the leaf and by their softer more herbaceous texture. The epidermal cells and stomata (Fig 12; Table 1) are smaller than in the previous two species.

The sporophylls tend to be confined to the base of the leafy part of the shoot and are generally rather shorter than the neighbouring sterile leaves. The synangia are rounded and the spores are the smallest found amongst the material from the Solomon Islands (see Table 1).

Discussion: This new species is distinguished chiefly by its ovate-lanceolate leaves which are arranged in two lateral series, its sporophylls which are shorter than the neighbouring leaves and found only towards the base of the aerial shoot and by its small spores. It resembles *T. lanceolata* Dang. of New Caledonia in its biseriate arrangement of the leaves, anatomy and sporophylls, which are towards the base of the leafy shoot and shorter than the neighbouring sterile leaves. In addition a spore illustrated by Sahni (1925) from the New Caledonian material matches in size almost exactly spores measured from *T. solomonensis*. It is however, not the same species. The New Caledonian species is a larger and more robust plant with thicker leaves which are broadly lanceolate or ovate and taper gradually to a point.

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